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AGRICULTURAL VALUE OF IMPERMEABLE SEEDS

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INTRODUCTION

During the years 1909 to 1916, inclusive, many germination tests of lots of clover and alfalfa seed were made for the purpose of determining the agricultural value of the impermeable seeds. A smaller number of tests of winter vetch, okra, and other seeds were made for the same purpose.

Impermeable seeds, in the sense in which the term is used in this paper, are seeds whose coats are impermeable to water at temperatures favorable for germination. In the majority of plants which produce impermeable seeds this feature of the seed coat results from the peculiar character of its outer layer of cells, which may, in addition, be covered by a continuous cuticle.

Such seeds have been oescribed by numerous investigators, including the present author, under the term "hard seeds." Guppy (9)¹ has, however, introduced a more appropriate term, "impermeable seeds," which will be used in the present paper. The term is relative, as impermeable seeds are capable of becoming permeable. While in the impermeable condition they remain very hard and dry, even when surrounded by water. When they become permeable, they absorb water readily, becoming soft and swollen. Naturally no seed can germinate while in the impermeable condition. In speaking of the germination of impermeable seeds, therefore, one means simply the germination of seeds which were impermeable at some previous time.

Many species of plants produce both impermeable seeds and seeds whose coats are readily permeable to water at one or more points. According to Guppy (9), these two types of seed can easily be distinguished by structural differences in certain plants (Entada polystackya and Axyris amaranthoides), but this is not true of any of the plants considered in this paper.

Verschaffelt (18) has investigated the relative permeability to both water and other liquids of different areas of the seed coats of a large

1 Reference is made by number to "Literature cited," p. 796.

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Vol. VI, No. 20 Aug. 14, 1916 G—01 number of plants which produce impermeable seeds. The present author has found that many of the seeds of the species of plants considered in this paper are more readily permeable to water in the region of the chalaza than elsewhere.

Nobbe and Haenlein (16), Gola (8), Ewart (7), Rees (17), and Guppy (9) have given us a good idea of the distribution among the natural plant families of species which produce impermeable seeds. All agree upon the Leguminosae as far surpassing all other families in this respect. Many other families also contain species which produce impermeable seeds.

OCCURRENCE OF IMPERMEABLE SEEDS IN CULTIVATED SPECIES

The peanut (Arachis hypogaea) excepted, probably all commercially important legumes cultivated in the United States produce a greater or less percentage of impermeable seeds. The percentage is small or fails entirely with spring vetch (Vicia sativa L.), some varieties of soybeans (Soja max (L.) Piper), kidney beans (Phaseolus vulgaris L.), Lima beans (Phaseolus lunatus L.), garden peas (Pisum sativum L.), and the newly introduced black bitter vetch (Vicia ervilia (L.) Willd.).

Table I shows the percentage of impermeable seeds in the commercial samples of a number of small-seeded legumes which have been tested by the Seed Laboratory during the six years 1904 to 1909.

Table I.—Percentages of impermeable seeds in small-seeded legumes tested during the years 1904 to 1909

	Number of	Percentage of impermeable seeds.					
Kind of seed.	lots tested.	Maximum.	Minimum.	Average.			
Red clover (Trifolium pratense L.)	1,642	46		G. C			
Alsike clover (Trifolium hyridum L.)	304	40	0	IC. 10			
White clover (Trifolium repense L.)	125	38	0	17. 30			
White sweet clover (Melilotus alba Desv.)	37	87	1.5	42.3			
Alfalfa (Medicago sativa L.)	1,737	72 68	0	13.5			
Winter vetch (Vicia villosa Roth.)	30		o.	20.9			
Spring vetch (Vicia sativa L.)	28	8	0	0.0			
Cowpea (Vigna sinensis (Torner)Savi) 1	37	60	0	3- 5			
Toothed bur clover (Medicago hispida denticulata (Willd) Urban)	6	85	9	48. o			
Spotted bur clover (Medicago arbica (L.) Huds.) 2	9	92	35	71.6			
Yellow-flowered sickle lucern (Medicago sativa falcata (L.) Döll) 1	5		35-5	49-7 10-4			

¹ Only two years' tests.

Recent investigations by the author (10) show that the first four species of plants in Table 1 produce very much higher percentages of impermeable seeds than are indicated and that many of the seed costs become permeable to water during the operation of bulling the seeds.

Important nonleguminous plants which produce impermeable seeds are okra (Hibiscus esculentus L.) and hollyhock (Althea rosea (L.) Cav.), both

² Only one year's tests.

belonging to the Malvaceae, atriplex (Atriplex spp.), of the Chenopodiaceae, alfilaria (Erodium cicutarium (L.) L'Hér.), of the Geraniaceae, asparagus (Asparagus officinalis L.), of the Convallariaceae, morning-glory (Ipomea purpurea (L.) Lam.), of the Convolvulaceae, and canna (Canna indica L.), of the Cannaceae. The cherry-tomato (Physalis pubescens L.), of the Solanaceae, occasionally has some impermeable seeds.

LONGEVITY OF IMPERMEABLE SEEDS

Although stating that some seeds with readily permeable coats may retain their vitality for many years in dry air, Ewart (7) was inclined to attribute extreme longevity of seeds in the soil exclusively to the impermeability of the seed coats. In contrast to Ewart's conclusion the work of Duvel, Beal (1–5), and others indicates that great longevity of seeds even in moist soil may sometimes be the result of factors entirely independent of an impermeable seed coat. There is no doubt, however, that the possession of such a seed coat contributes to the length of life of the seed by decreasing or entirely preventing respiration and imbibition and, in general, by reducing the rapidity with which all physical and chemical changes take place within the seed. The seeds which Ewart (7) and Rees (17) have shown to retain their viability for 15 to 50 years or longer are almost exclusively seeds with impermeable seed coats. Beal, however, found the seeds of some typically permeable seeds (for example, Brassica nigra) viable after 30 years in the soil.

Becquerel (6) has reported the germination of impermeable seeds of three leguminous plants over 80 years old, and Ewart (7) mentions several plants as germinating from 5 to 80 per cent when over 50 years old.

According to Ewart, the curves of viability based on the germinating capacity of seeds of known age suggest 150 to 250 years as the probable extreme longevity of any known seed.

EXPERIMENTAL WORK DURING 1909-1916

The major part of the work reported in this paper was done with the seeds of red clover, alsike clover, white clover, white sweet clover, alfalfa, hairy vetch (Vicia villosa Roth.), and okra. A small amount of work was done also with seeds of crimson clover (Trijolium incarnatum L.), black locust (Robinia pseudacacia L.), kidney bean (Phascolus vulgaris L.), garden and field peas (Pisum sativium L.), cowpeas, and Chamacerista nicitans L. Muench.

Nearly all chamber tests and greenhouse tests were made with two samples of 100 seeds each from each lot of seed tested. In some cases the number available was small and less than 200 seeds were used. A number of tests of okra were made with two lots of 50 seeds each. In the

¹ Unpublished data

field from 250 to 500 seeds were used in testing each lot, 500 being tested in nearly every case.

In all of the germination tests which were conducted in the germinating chambers folded blue blotting paper free from soluble dye was used as germinating beds for the seeds of the clovers, alfalfa, black locust, and Chamaecrista nicitans, and folded canton flannel for the seeds of the other kinds of plants. In the green house tests both sand and steam-sterilized potting soil were used.

VIABILITY OF IMPERMEABLE SEEDS

In May and June, 1914, 128 lots of seed from 1 to 5 years old were tested for germination, and the viability of the seeds remaining impermeable after six days was determined and compared with the viability of the seeds which softened in the first six days of the test.\(^1\) Table II summarizes the results.

Table II .- Viability of impermeable seeds from 1 to 5 years old

			Average per	centage of-	
Kind and age of seed.	Number of lots.	Germina- tion.	Imperme- able seeds.	Viability of imperme- able seeds.	Viability of seeds which softened in six days.
Red clover:					
ς years	21	34	59	99	83
4 years	5	43	43	96	75
3 years	9	34	58	99	81
2 years	11	39	60	99	98
1 year	8	26	74	100	99
Alsike clover:					1
3 years	4	15	81	100	79
2 years		7	90	100	70
I year	5	6	90	100	to
White clover:					1
3 years		8	82	95	44
2 years		8	90	100	50
ı year	4	12	87	100	92
Sweet clover:	1		1	Ì	
4 years		1.5	98	100	7.5 80
2 years	. 12	4	95	98	
1 year	. 3	10	89	100	91
Alfalfa:		i			
3 years		71	25	100	G5
2 years		69	28	100	99
r year	. 7	67	32	100	1 "
Hairy vetch:				1	: 6:
5 years		57	8	100	
ı year		59	17	100	71
Crimson clover: 2 years		65	26	02	6:
Okra: 3 years	. 5	9	87	92	1 1
Chamaecrista nicitans:	1		1	85	6
4 years	. 1	36	43	1 %	1 "
Robinia pseudacacia:		[1	0.5	1 5
At least 5 years	. I	25	54	95	. *

¹ To determine the viability of the impermeable seeds, the seed coats of 20 seeds from each lot of all seeds remaining impermeable after six days if not more than 20) were cut with a kmile, and these seeds with cut seed coats were then subjected to germination conditions for seven days.

Over 90 per cent of the impermeable seeds were viable in every case, except the lot of seed of Chamaecrista nicitans. In most cases 100 per cent were viable. The average percentage of viability of the impermeable seeds was invariably greater than of the seeds which softened within six days. The difference ranged from 1 per cent to over 50 per cent—the latter with 3-year-old white-clover seed—and in general increased with the age of the seed.

RATE OF SOFTENING OF IMPERMEABLE SEEDS WHEN KEPT IN WET BLOTTERS

Table III shows the average rates of softening of seeds which had remained impermeable after 10 days in wet blotters. These seeds were kept in wet blotters for three years.

TABLE III Rate of softening	of impermeable seeds	when kept in wet blotters
-----------------------------	----------------------	---------------------------

Kind of seed.	Description,1	No, of	Average percentage of seeds im-	Average percentage of im- permeable seeds as shown in preceding column which sol- tened in time indicated.				
			permeable after 10 days.	month.	t year.	years,	years.	
Pod alovet	Hand-gathered	20	86	Q	10			
Do.	Commercial	6	11	0	30	. 44	55	
Aleiles alerror	Hand-gathered		1 i	9	27	45	55	
			91	9 ;	52	63	66	
	Commercial	. 5	14	7 :	21	28	28	
	do	5	30	3 .	1.3	23	30	
Sweet clover	Hand-gathered	. 2	97	5	27	3.5	44	
Do	Commercial	- 4	24	Š	21	20	37	
	Hand-gathered		70	46	97	99	100	
1)0	Commercial	. 8	20	10	70			
	Hand-gathered		a 65				95	
	do			13 :	85	97	98	
			45	42	93	100		
	Commercial	5	12	50	100			
Okra	do	5	a 56	34	01	- 06	98	

¹ All hand-gathered lots of seed were gathered and hulled by hand a few days before the beginning of the tests. Commercial lots were of uncertain age, probably in most cases a little less than 1 year old.

- 1. Less than 10 per cent of the seeds of red clover, alsike clover, white clover, and sweet clover which remained impermeable after 10 days softened in one month; and from about one-third to a little over one-half of them softened in three years.
- 2. Nearly all of the impermeable seeds of alfalfa, hairy vetch, okra, and crimson clover which remained after 10 days softened in one year in wet blotters, but a very few of all except crimson clover remained impermeable after three years. There is a marked contrast in this respect between these species of plants and those named in the preceding paragraph.
- 3. The impermeable seeds in hand-gathered lots of alsike-clover seed and alfalfa seed softened much more rapidly than the impermeable seeds

in commercial lots of seed of the same plants. There was but little difference in this respect between the impermeable seeds of hand-gathered lots and commercial lots of the other species of plants.

Almost all of the seeds of each kind of plant which softened at any time during the three years germinated and produced vigorous seedlings.

Besides seeds of the species given in Table II a few impermeable seeds of kidney bean, garden pea, and cowpea were included in the tests. All of the beans and peas softened and germinated within three mouths, and all of the cowpeas within eight months.

INFLUENCE OF MATURITY ON THE RATE OF SOFTENING OF IMPERMEABLE
RED-CLOVER AND ALSIKE-CLOVER SEEDS IN WET BLOTTERS

The lots of hand-gathered seed included under Table III were thoroughly mature and dry in the heads before being removed from the plants. Figure 1 shows graphically the comparative rates of softening of such well-matured impermeable red-clover seed and of impermeable red-clover seed of two other degrees of maturity.

Seven of the eight lots of slightly immature seed were gathered at the same time and from the same cultivated rows of plants as were seven of the eight lots of mature seed, the former being taken from heads which were slightly green and succulent, the latter from black, dry heads. The three lots of light, immature seed used in the comparison were separated from three of the lots of slightly immature seed by a gravity blowing machine. Only seeds of good appearance, though frequently of small size in the immature lots, were used in the tests.

The average percentages of the mature seeds, the slightly immature seeds, and the more immature seeds which remained impermeable after 10 days in wet blotters and from which the rates of softening were calculated were respectively 84, 72, and 27.

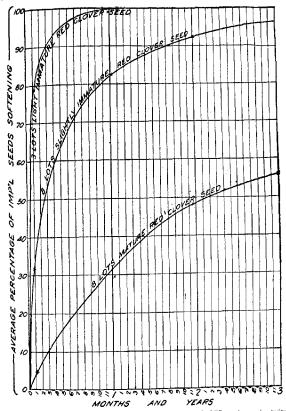
Of the impermeable seeds from lots of light, immature seed, 78 per cent softened in one month and 100 per cent in 13 months. In contrast to this, only 5 per cent of the impermeable seeds from lots of well-matured seed softened in one month and 44 per cent of them remained impermeable after three years.

The differences in the rate of softening of impermeable seeds from lots of mature and immature seeds of alsike clover were similar to those shown for red-clover seed. No other species of plants were investigated for rate of softening.

Hiltner (11) has shown that the percentage of impermeable seeds and the rate at which they soften when placed under conditions favorable to imbibition may in some cases be greatly altered by previous drying. Although only seeds which seemed to be thoroughly dry were used in these experiments, it is possible that artificial desiccation of the less mature lots would have increased the percentages of impermeable seeds and de-

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creased the rate at which they softened. As will be shown later, however (p. 775), moderate heating of thoroughly air-dried seeds of these plants has little or no effect under ordinary conditions.



Fro. 1.—Curves showing the rate of softening of impermeable red-clover seeds of different degrees of maturity.

ESTIMATION OF THE GERMINABILITY OF IMPERMEABLE SEEDS

It is evident from the preceding discussion that it is impossible to estimate in advance what proportion of the impermeable seeds of a given lot will germinate under ordinary germination conditions in any given length of time. At one time Nobbe (14) proposed that one-third of the seeds of red clover remaining impermeable after 10 days be reckoned as capable of germinating in one year. He later tested in distilled water 66 lots of red-clover seed from various sources, using 1,000 seeds of each lot. From 2.4 to 90 per cent of the seeds of the different lots which remained impermeable after 10 days softened in

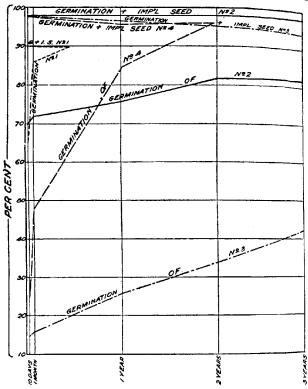


Fig. 2.—Curves showing the rate of softening and of germination of impermeable red-clover seeds of different lots.

distilled water in one year. On the basis of these results Nobbe (15) abandoned his previous position as untenable.

Different lots of seeds of any one of the species of plants included in Table III illustrate differences in the rate of softening of the impermeable seeds which are comparable to those reported by Nobbe. Figure 2

shows graphically the differences in this respect between four lots of redclover seed. Lot 2 was commercial seed, while the other lots were seed which had been gathered and hulled by hand. While lot 3 was thoroughly dry when gathered, lots 1 and 4 were gathered when the heads were slightly green.

The lower of each pair of lines indicates the progress of germination of one lot of seed, the upper line the sum of percentages of germination and of impermeable seeds, and the space between the two lines of the pair the percentage of seeds which were impermeable at any given time.

- 1. All of the seeds of lots 1 and 4 softened and practically all germinated in, respectively, six months and two years. Yet only about 40 per cent of the impermeable seeds of lots 2 and 3 softened and germinated in three years.
- 2. Since the percentages of seeds of lots 1 and 4 which remained impermeable during the first 10 days were about the same as of lots 2 and 3, it is evident that the original percentage of impermeable seeds bears no relation to the rate at which these will soften or germinate.
- 3. It should be emphasized that the differences in maturity of the different lots of seed were not noticeable in the appearance of the seeds and offered, therefore, no basis for estimating the percentages of impermeable seeds which the different lots contained or the rates at which these impermeable seeds would soften.

RATE AT WHICH IMPERMEABLE SEEDS BECOME PERMEABLE WHEN STORED IN MANILA ENVELOPES

Hand-gathered, hand-hulled seeds were tested for germination and impermeable seeds after being stored in manila envelopes for different lengths of time. The first test of each lot was begun a few days after the seeds were harvested, and the last test in some cases more than 4½ years later.

Table IV shows the calculated average percentages of the originally impermeable seeds in some of these lots of seed which became permeable in one month, one year, two years, three years, and four years. Loss of permeability during storage is indicated by the minus (-) sign.

- r. The impermeable seeds of red clover, alsike clover, white clover, and sweet clover became permeable very slowly in dry storage. The red-clover seed changed more rapidly than the other kinds of clover seed, but less than one-half of the impermeable seeds of this species became permeable in four years.
- 2. The percentages of impermeable seeds in lots of alsike-clover, white-clover, and sweet-clover seed gathered in 1912 increased slightly during the first year and then remained about constant during the second year. This initial increase is probably due to the seed's being tested the first time before it was thoroughly dry. A similar increase occurred in a few lots of red-clover and alfalfa seed.

Table IV.—Rate at which impermeable seeds became permeable when stored in manila envelopes

Kind of seed.	Year in which grown.	Num- ber of lots.	Average percent- age of imper- meable seeds		ted aver eable see in which indicated	age perc eds as sh h becan i,	entage of own in p ne penno	the im recedin cable is
			when gath- ered.	month.	year.	years.	years.	years.
Red clover	1909	12 5 9	89 81 86	0	14 22	41	33	3
Alsike clover	1911 1912 1912	6 6	85 86 88	-2	9 - 5	- 3 - 2	34	
Sweet clover	1912 { 1911 1912	6 4	85 80 60	2	-12 24	-12 70 55		
Hairy vetch	1909	a I	73 60		82		90	

^a This lot of hairy-vetch seed was grown by the Office of Foreign Seed and Plant Introduction, Bureau of Plant Industry, at Chico, Cal.

3. Impermeable alfalfa and hairy-vetch seed ¹ became permeable more rapidly than impermeable clover seed, 82 per cent of one lot of hairy-vetch seed becoming permeable in one year.

Besides the kinds of seed given in Table IV, five lots of okra seed gathered in 1911 were tested when fresh and six months, two years, and three years later. When fresh, all seeds softened and an average of 98 per cent germinated. Six months later only 23 per cent germinated and 71 per cent were impermeable. During the following two and one-half years very little change in permeability occurred.

It should be added that there was a slight decrease in the viability of the red-clover seed during the third and fourth years, and a large decrease in the viability of the vetch seed during the fourth year.

VARIATION IN THE RATE AT WHICH IMPERMEABLE SEEDS OF A SINGLE SPECIES BECOME PERMEABLE

The impermeable seeds in some of the lots included in Table IV became permeable in dry storage much more rapidly than those of other lots of the same kinds of plants. In fact, the percentage of the impermeable seeds in different lots of red-clover seed which became permeable in four years varied from about 15 to about 80. This variation is further emphasized by the results of tests conducted in the fall and winter of 1914–15 and in September and December, 1915, using

¹The vetch seeds in the lots here considered were thoroughly dry and black when first tested. Vetch seed, while it remains green in color and has a high water content, contains but a small percentage dispermeable seed or none. This percentage increases in storage for a time before any decrease takes place.

exclusively seeds grown in 1914. Table V shows the average percentages of the viable seeds which were impermeable in the two tests and the calculated average and maximum percentages of the seeds, impermeable when freshly gathered, which became permeable in the interval of about one year between the two tests.

TABLE V.—Change in permeability of clover and alfalfa seeds during the first year after harvesting

Kind of seed.	Manner of hulling.	Number of sam- ples.		de seeds were im-	ages of imperm fresh,	ed percent- the seeds, cable when which be- rmeable in year,
			Fresh.	ı year oki.	Average.	Max- imum.
Red clover. Do. White clover. Do. Sweet clover. Alfalfa.	Hand Machine. Hand	220 207 12 37 8 5 6	92 17 91 18 98 34 98 32	87 14 91 16 90 28 98	6 19 0 10 8 18 0 60	52 1 40 1 26 55 1 40

¹ These calculations are based only on lots of which 30 per cent or more were impermeable when tested the first time.

The hand-hulled lots contained very large percentages and the machine-hulled lots comparatively small percentages of impermeable seeds. With few exceptions in the case of single lots of seed, the impermeable seeds in the hand-hulled lots became permeable more slowly than those in the machine-hulled lots.

The average results for all lots showed that not more than 8 per cent of the impermeable seeds in hand-hulled lots of the different kinds of clover seed had become permeable during the interval between the two tests; yet over 50 per cent of the impermeable seeds in one lot each of hand-hulled red-clover seed and hand-hulled white-clover s. d became permeable.

The case of the hand-hulled white-clover seed is especially interesting. Eight lots averaged 98 per cent of impermeable seeds when fresh. Only 1 per cent of the impermeable seeds in seven of these lots became permeable in a little over a year. Of the impermeable seeds in the other lot 36 per cent became permeable in two months, 45 per cent in three months, and 55 per cent in 14 months. Nothing in the appearance of the different lots of seed either of white clover or of the other kinds indicated that any differences would be found in the rate at which the impermeable seeds became permeable.

¹The results of the special investigation on impermeable clover seed conducted in the fall and winter of 1914-15 have been published elsewhere (10).

It should be added that no change could be detected in the viability of the seeds during the interval between the two tests except in ease of the machine-hulled lots of red-clover seed and of alfalfa seed. With these there was a very slight decrease in viability.

INFLUENCE OF MATURITY ON THE RATE AT WHICH IMPERMEABLE RED-CLOVER SEEDS BECOME PERMEABLE IN MANILA ENVELOPES

Four lots of red-clover seed were gathered in July, 1910. This w_{as} the earliest seed of a good grade that could be obtained from the plants in question. Four other lots of seed were gathered from the same cultivated rows of plants in October, 1910.

The average percentages of impermeable seeds in the lots of seed gathered in July and in October were, respectively, 71 and 82. When again tested for germination two years later, the average percentages of impermeable seeds were 35 and 62. In other words, one-half of the impermeable seeds in the less mature lots which were gathered in July and one-fourth of those in the more mature lots which were gathered in October became permeable in two years. There was practically no change in viability during the two years.

COMPARATIVE RATES AT WHICH IMPERMEABLE SEEDS BECOME PERMEABLE IN WET BLOTTERS AND IN DRY STORAGE

A comparison of Tables III and IV shows that impermeable seeds become permeable more rapidly when kept under germination conditions than when stored dry. The difference in rates varies widely among different lots of the same species.

Between 20 and 40 per cent more of the majority of the lots of handhulled red-clover seed remained impermeable after four years in dry storage than after four years in wet blotters. With a few lots of redclover seed, however, the differences were less than 5 per cent, and with a few other lots the differences were between 50 and 60 per cent.

Figure 3 represents graphically the changes in the percentage of impermeable seeds of typical lots of red clover, alsike clover, sweet clover, and alfalfa seed when kept in wet blotters and when stored dry in manila envelopes for various periods.

- 1. With each species the percentage of impermeable seeds decreased more rapidly in wet blotters than in dry storage.
- 2. The percentage of impermeable seeds decreased more rapidly during the first year than during succeeding years both in wet blotters and in dry storage.

PRODUCTION OF SEEDLINGS IN SOIL BY IMPERMEABLE LEGUMINOUS SEEDS

Comparative tests were made in germinating chambers, in a greenhouse, and in soil outdoors, using lots of seed with varying percentages of impermeable seeds. The results of these tests indicate that, with rare

exceptions, very few of the impermeable seeds of the different kinds of clover, except crimson clover, will produce seedlings in the soil even in three months at temperatures such as prevail in late spring or in summer.

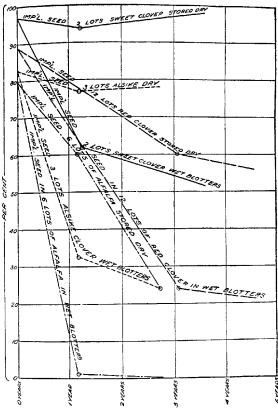


Fig. 3.—Curves showing the changes in the permeability of seeds in wet blotters and in dry storage for various periods.

The case of alfalfa, crimson clover, and the larger-seeded species is different. It was calculated that varying percentages of the impermeable seeds of alfalfa, hairy vetch, Canada field pea, cowpea, and okra produced seedlings in a few days or weeks both in a moderately warm

greenhouse and in greenhouse flats in which tests were conducted out-

In one experiment it was calculated that 16 per cent of the impermeable red-clover seeds, 5 per cent of the impermeable white-clover and sweet-clover seeds, and 38 per cent of the impermeable alfalfa seeds produced seedlings in greenhouse flats in three months. In the same time 5, 2, 3, and 8 per cent, respectively, germinated in a germinating chamber at room temperature, the rest remaining impermeable.

On June 7, 1909, seeds remaining importable during germination tests in germinating chambers were sowed in soil in large greenhouse flats, which were then set outdoors in the warm space between two greenhouses. The soil was kept watered, and observations were continued until November 30, 1909. During the latter half of November the temperature fell below freezing several times, but the last few days of the test were warm. The results of the tests are summarized in Table VI.

Table VI.—Production of seedlings by leguminous seeds which remained impermeable during germination tests

Kind of seed and test No.	Number of seeds	Percentage of seeds which produced seedlings in-					
	used.	ı montlı.	2 months.	3 months.	6 months.		
Red clover:							
58593	110	5	7	8	8		
83583	109	12	16		28		
83843		3	5 7	5	5		
85272 8534I	87 43	5 5	5	. 7 5	9		
85371	30	17		23	3, 16		
85454	25	8	23 8	12	16		
Average		6	10	11	, I4		
Sweet clover:							
78539	195	3	4	4	e 14		
Alfalfa:					i		
62874		75	92	92	Ç2		
78479		53	57		50		
85276	30	80	90	90			
Average		. 69	80	80	80		
Hairy vetch:	1						
78326	24	38	38	. 38	38		

^a During the first 5 months of the experiment 4 per cent were produced; the remaining 10 per cent during the last few days of the experiment, following the freezing of the soil.

Only 14 per cent of the impermeable sweet-clover seeds and an average of 14 per cent of the impermeable red-clover seeds produced seedlings in six months.

2. An average of 69 per cent of the impermeable alfalfa seeds produced seedlings in one month, and an average of 80 per cent in two months. after which only one new seedling appeared in the next four months.

3. Thirty-eight per cent of the one lot of impermeable hairy-vetch seeds produced seedlings in one month, after which no new seedlings

appeared.

4. It is worthy of notice that after four months, during which no new sweet-clover seedlings appeared, 10 per cent of the seeds used produced seedlings in a few days following the cold weather in November. This is particularly interesting in the light of subsequent results.

EFFECT OF DIFFERENT CONDITIONS UPON THE GERMINATION OF IMPER-MEABLE SEEDS IN SOIL

It has been shown that some seeds which would be reported as impermeable according to the chamber tests will produce seedlings in a comparatively short time in the soil. Experiments were conducted to determine the effects of separate factors.

Comparative tests showed that neither moistening the blotters which were used for germinating bed with strong aqueous soil extracts nor the alternate wetting and drying of the seeds at frequent intervals affects the rate of softening of impermeable clover seeds.

Neither the depth of planting nor the firmness of the soil nor the conservation of surface moisture by shading affected the precentage of seedling production by impermeable clover and alfalfa seeds in greenhouse tests, except when the seeds were planted over 34 inch deep. Fewer seedlings reached the surface of the soil from seeds planted 1 inch deep than from seeds planted 1/4 to 3/4 inch deep.

On the other hand, certain factors influenced the softening of impermeable seeds and would probably affect the production of seedlings in the soil. These factors will be considered in the following sections.

EFFECT OF HIGH TEMPERATURES UPON THE GERMINATION OF IMPERMEABLE CLOVER AND ALFALFA SEEDS

DRY HEATING.—Storing seeds for 6 months in a dry atmosphere at 45° C. slightly increased the subsequent germination of previously impermeable alfalfa seeds, but had no effect upon impermeable seeds of red clover or sweet clover. These results differ from results obtained by Hiltner (11). This author found that drying red-clover seed for eight days at 35° slightly increased both the percentage which remained hard after a 10-day germination test and the percentage which softened but did not germinate.

Heating at 50° C. for 21 hours had no effect upon the softening or germination of impermeable seeds of red clover or sweet clover when later subjected to a germination test.

HEATING IN WET BLOTTERS.—Seeds which remained hard after a 6-day germination test at 24° C. were subjected in the wet blotters to a temperature of 36° for the following seven days, during which time duplicate lots remained at 24°. Table VII shows the average percentages which germinated, and which softened but did not germinate.

Table VII.—Softening and germination of impermeable clover and alfalfa seed and at 36° C.	s at 24
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Kind of seed.	Number of lots.	Number tested		Average p of germina	ercentage ation at—	Average which so did not at—	percentage oftened but genuinate
		24° C.	36° C.	24° C.	36° C.	24° C.	35° C.
Red clover. Alsike clover. White clover. Sweet clover. Alfalfa. Crimson clover.	60 15 11 17 18 2	3, 220 1, 089 826 1, 604 519 48	3, 227 1, 068 820 1, 607 516 56	0. 48 1. 07 . 41 . 94 6. 31 1. 92	1. 53 6. 06 . 51 . 94 10. 14 18. 27	0. 0g . 15 0 . 06	0. 34 . 99 I. 34 . 45 . 22 . 96

- 1. A larger percentage of the seeds softened at 36° than at 24°. C. The differences were small with red-clover, white-clover, and sweet-clover seed, somewhat larger with alsike-clover and alfalfa seed, and over 16 per cent with crimson-clover seed.
- 2. With the exception of white-clover seed at 36° C. nearly all the seeds which softened germinated. However, a somewhat larger proportion of the seeds which softened failed to germinate at 36° than at 24° .

In view of the very slight effect of heating at 36° C, for seven days in wet blotters, it hardly seems possible that soaking clover seeds over night in water at 34° before planting can bring about the germination of impermeable seeds as suggested recently by Müller (13).

EFFECT OF FREEZING TEMPERATURES ON THE GERMINATION OF IMPERMEABLE LEGUMINOUS SEEDS

One instance has already been mentioned in which impermeable sweet clover seeds previously lying dormant in the soil produced seedlings after a few days of freezing weather. (See Table VI.) A series of experiments was begun late in December, 1909, to test further the effect of freezing temperatures on the subsequent germination of impermeable leguminous seeds. The seeds used had lain in water without softening for 13 to 5 months previous to the beginning of the experiment.

Different lots of the seeds were tested in a germinating chamber at about 20° C., in very moist soil in drinking glasses which were covered with black paper to exclude the light, and in soil in greenhouse flats. All of the seeds were subjected to freezing temperatures either before or during the germination tests, as follows:

The seeds which were tested in a germinating chamber at 20° C. were previously subjected, either dry or in small vials of water, to a temperature of about -10° C. One lot of each sample was given this treatment for 9 days and another lot during two periods of 9 days and 16 days, respectively, with an intervening period of a few hours in the laboratory at ordinary room temperature. As one exposure to this temperature had practically the same effect as two such exposures, only the average results of the tests of the two lots are herein considered.

TABLE VIII .- Germination of impermeable leguminous seeds with and without freezing

Kind of seed.	Test No.	Germination, impermeable seeds, and dead seeds.	Check test in cham- ber.	Tested in cham- ber after freez- ing in dry condi- tion.	Tested in cham- ber after freez- ing in water.	Tested in soil on window ledge; frozen during test.	Tested in soil in green- house flats; frozen during test.
	,	Percentage of ger- mination.	6	8	26	21	
	85262	Percentage of im- permeable seeds.	93	92	72	65	
		Percentage of dead seeds.	1	٥	2	14	
Red clover	[[Percentage of ger- mination.	5	13	9	32	38
	85272	Percentage of im-	94	85	85	57	.
, ,		permeable seeds. Percentage of dead	1	2	6	11	
		Percentage of ger-	12	14	10	17	50
Alsike clover	84087	mination. Percentage of im-	87	82	80	72	
Alsike clover 84	04007	Percentage of dead	1	4	10	11	}
		seeds. Percentage of ger-	3	10	11	IO	30
White clover	85192	mination. Percentage of im-	96	89	. 88	81	
	-3-9-	permeable seeds. Percentage of dead	1	1	I	9	
		Seeds. Percentage of ger-	2	1	1	4	74
Sweet clover	78539	mination. Percentage of im-	97	99	98	78	
	1-309	permeable seeds. Percentage of dead	r	٥	1	18	
		Percentage of ger-	4	20	14	6	56
Alfalfa	78479	mination. Percentage of im-	95	80	84	84	
mana	10419	permeable seeds. Percentage of dead	ı	0	2	10	
		Percentage of ger-	1	14	7	2	8
Black locust		mination. Percentage of im-	99	84	90	96	ļ
		permeable seeds. Percentage of dead seeds.	o	2	3	2	

The seeds in the drinking glasses were so placed that they could be examined through the glass. The drinking glasses were kept on a shaded window ledge outside the laboratory during two periods of 10 days and 14 days, respectively. Each of these periods included several cold days during which the soil became frozen clear to the bottoms of the glasses. During an intervening period of 9 days and again after the second period on the window ledge they were kept in the laboratory at ordinary room temperature.

The greenhouse flats were kept outdoors during the entire experiment. The soil in them was alternately frozen and thawed at intervals during the first two or three months.

Check tests were made in a germinating chamber at about $_{20^\circ}$ C without previous treatment of the seeds.

All of the tests were continued until March 24, 1910, and those in the greenhouse flats until May 7, 1910.

Table VIII shows the percentages of the seeds which germinated or produced seedlings in the different tests, the percentages which remained impermeable, and the percentages which softened but did not germinate in all of the tests except those which were conducted in greenhouse flats.

r. Subjection to a freezing temperature previous to the germination test slightly increased the percentages of the impermeable red-clover, white-clover, alfalfa, and black-looust seeds which germinated. In some cases, especially when the seeds had been frozen in water, this treatment increased also the percentages which softened but did not germinate. This latter effect is partly the result of the fact that a part of the seeds which softened after the first period of freezing were killed by the second freezing.

The impermeable sweet-clover seeds were wholly unaffected by this treatment.

- 2. The effect of freezing the impermeable seeds in soil in drinking glasses was similar to but greater than the effect of subjecting them to a freezing temperature previous to a germination test in a germinating chamber. Nearly all of the seeds which softened following each period upon the window ledge softened during the first few succeeding days in the laboratory.
- 3. The percentages of the impermeable seeds of the clovers and alfalfa which produced seedlings in the greenhouse flats with frequent freezing and thawing were much greater than the percentages which germinated in the germinating chamber or in the drinking glasses. This was particularly noticeable with the sweet-clover and alfalfa seeds. Nearly all of the seedlings appeared during warm days immediately following freezing weather.

Only 8 per cent of the impermeable black-locust seeds produced seedlings, and these few seedlings appeared after settled warm weather had begun late in March. REFECT OF ALTERNATIONS OF TEMPERATURE ON THE GERMINATION OF IMPERMEABLE CLOVER AND ALFALFA SEEDS

Seeds remaining impermeable after from 4 months to over 12 months in wet blotters were kept in a chamber at room temperature for 49 days. The seeds were then kept for 50 days in chambers which, during a large part of the time, were heated daily to about 30° C. and then allowed to cool slowly to room temperature. Finally the seeds were again kept in chambers at room temperature for 51 days. Table IX summarizes the germination records for these three successive periods.

TABLE IX.—Germination of impermeable clover and alfalfa seeds during successive periods of similar length with different temperature conditions

		Approximate percentages of ger- mination during—					
Kind of seed.	Number of imper- meable seeds used.	49 days at room tem- perature.	quent	room tem-			
Red clover. Alsike clover. White clover. Sweet clover. Alfalfa.	118 270 637	3 0 1 2 25	7 2 2 1 21	1 1 1 1 7			

The use of the alternating temperatures increased very slightly the germination of red-clover, alsike-clover, and white-clover seed, but did not influence the germination of sweet-clover and alfalfa seed. In no case did more than 11 per cent of the impermeable clover seeds germinate in the five months included in the three periods of observation.

Clover seeds which remained impermeable after various lengths of time in wet blotters were tested for germination at 1° C. in an ice box averaging about 10°, at 20°, at 30°, and with daily alternations between each two of these temperatures. When alternations of temperature were used, the seeds were kept in the chamber at the warmer temperature for about seven hours of each day and in the chamber at the cooler temperature the remainder of the day. In each test a succession of several temperature conditions was used, each condition being maintained for several days.

Figure 4 shows graphically the results of a scries of tests of red-clover seeds from a single original lot which remained impermeable after four days' soaking in water. During these tests many seeds softened and remained for several days after softening at a temperature too cold for their germination. These softened seeds, as well as those which softened at warmer temperatures, invariably germinated later if subjected to a temperature favorable for germination. In order to emphasize the effects of the different temperatures, figure 4 shows only the rates of softening of the seeds without regard to their immediate germination.

During the first few days of the test from 5 to 7 per cent of the seeds softened under each temperature condition, showing that not all the easily permeable seeds had been removed by the previous soaking. After the first seven days the rate of softening varied according to the temperature conditions of the different tests.

r. When the alternation of temperatures from the ice box to 30° C was used after a period of incubation in the ice box the seed softened rapidly for a few days, but the rate of softening diminished greatly within a week and soon fell off almost entirely.

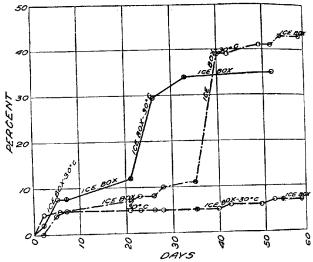


Fig. 4.—Curves showing the rate of softening of impermeable red-clover seeds under different temperature conditions.

2. While 32 per cent of the seeds softened when the alternation of temperatures was used after 35 days in the ice box, only 22 per cent softened with the same alternation after 14 days in the ice box.

3. When the alternation of temperatures followed 35 days at 30°, only 2 per cent softened in 19 days.

Results similar to those just outlined have been obtained with redclover, alsike-clover, white-clover, and sweet-clover seeds which had previously remained impermeable in wet blotters for from two years to five years. The alternation from 1° to 30° C. has been as effective as the alternation from 10° to 30°. The alternation from 1° or 10° to 20° has had somewhat less effect. In any case the effectiveness of an alternation has always depended upon a previous incubation of the seeds at a cool temperature. Usually the longer the previous period of cool incubation the greater has been the effect of the alternation. Alternations from 1° to 10° or from 20° to 30° had little or no effect.

In some cases more than 90 per cent of seeds which had previously remained impermeable in wet blotters for several years have softened and germinated in a few weeks with a favorable succession of constant cool temperatures and alternations of temperature.

The work outlined in this section is of special interest in connection with the following sections. The results here presented would lead one to expect that impermeable clover seeds would lie in the soil without change during either steady cold weather or constantly warm weather and in the fall, when an alternation of warm days and cool nights follows the hot summer months, but that many of them would germinate and produce seedlings at the beginning of the growing season in the spring when a similar alternation follows months of cold winter weather. These results also show that subjection to freezing temperatures is not necessary in order to prepare the majority of impermeable clover seeds for rapid germination. A temperature of about 10° C. does quite as well as 1°, and either of these temperatures is much more effective under favorable conditions than freezing temperatures under conditions which are less favorable. (See p. 776–778 and Table VIII.)

GERMINATION OF SEEDS AFTER PASSING THE WINTER ON OR UNDER THE PARENT PLANTS IN THE FIELD

Seeds which had passed one winter on or under the parent plants in the field were gathered the following spring after warm weather had begun. The germinating capacity of these seeds and the percentages which were impermeable were determined and compared with the germinating capacity and percentage of impermeable seeds of lots of seed which were gathered from the same stands of plants the preceding fall and stored in the laboratory during the winter

The red-clover seeds which were gathered in the spring consisted of eight lots from heads which remained intact upon the parent plants and were several inches above the ground, and eight other lots from heads which were embedded in the mud.

The alsike-clover, sweet-clover, and yellow-trefoil seeds gathered in the spring were all embedded in the mud. A large number both of these and of the red-clover seeds which were embedded in the mud had germinated and produced a dense growth of strong green seedlings before they were gathered. Many red-clover seeds had softened, and a few had germinated even in the heads which were several inches above the soil. About half an inch of soil was taken up with the seedlings which were growing in the soil, and carefully worked over to re-

move all the seeds. All seeds which had softened and looked healthy were counted as germinated.

The red-clover seeds which were impermeable when removed from the soil or from the seed heads were subjected to a germination test for one mouth in a chamber at about 20° C. The seeds which germinated in the germinating chamber were included with those which germinated in the soil in determining the germinating capacity.

All the alfalfa seeds gathered in the spring were from pods which remained upon the straw a foot or more above the soil. Ninety per cent or more of the seeds in these pods were brown and dead, and some were partly disintegrated. The remaining 10 per cent or less were bright, plump, and yellow. These were retained for the germination test. All alfalfa seeds which could be found in the surface soil under the plants were dead.

There were included in the examination 9,723 red-clover seeds, 575 alsike-clover seeds, 412 sweet-clover seeds, 200 alfalfa seeds, and 90 yellow-trefoil seeds, which were gathered in the spring.

Table X gives the results of the investigations.

TABLE X .- Germination of leguminous seeds after passing the winter on or under the parent plants in the field compared with the germination of seeds harvested the previous

			Avera	ge percenta	ge of—	Calculated average
Kind of seed.	Num- ber of lots.	Scason in which gathered.	Germina- tion.	Imperme- able secds.	Dead seeds.	percentage of the seeds previously imperme- able which became perme- able.
Red clover. Do. Do. Alsike clover. Do Sweet clover. Do. Alfalfa. Do. Yellow trefoil.	I I I I	Fall, 1909. March, 1910a. March, 1910a. March, 1912b. Fall, 1912c. April, 1913c. Fall, 1913 c. Fall, 1913 d. April, 1914d. April, 1914d.	59 10 63 76 3	88 33 61 84 37 90 36 22 97 35	4 1 2 1 4 0 1 2 0	

a From heads embedded in the soil; germination reported includes 1 month in chamber.
b From heads on the straw above the soil; germination reported includes 1 month in chamber.
c Germination in the field only.
d From dry heads well above the soil; germination in chamber.

From 52 to 63 per cent of the clover and yellow-trefoil seeds which were impermeable in the fall softened after passing the winter in the soil. Of the impermeable red-clover seeds which were in heads several inches above the soil 30 per cent softened. In the meantime only 1 per cent of the impermeable red-clover seeds which were stored in the laboratory over the winter became permeable, and the percentage of alsike-clover

and sweet-clover seeds which were impermeable increased under dry storage in the laboratory. Nearly all of the seeds which softened after wintering in the soil or on the plants germinated.¹

2. Only those alfalfa seeds which remained importmeable survived the winter on the plants. Only 3 per cent of those seeds gathered in the spring germinated and 97 per cent were impermeable. Of those gathered in the fall 76 per cent germinated and 22 per cent were impermeable, only 2 per cent being dead.

Additional tests were made upon self-sowed seed in February and March, 1916, taking advantage of the effect of a favorable alternation of temperatures upon the softening of the seeds (see p. 779-781), as follows:

One lot of self-sowed red-clover seed and two lots of self-sowed sweetclover seed, with the soil in which they were embedded, were gathered on February 29 and immediately placed in an ice box in which the temperature was constantly somewhat below 10° C. During the next few days the seeds were separated from the soil without allowing them to become dry at any time. Both before and after removing them from the soil they were daily alternated between the ice box and the germinating chamber at 30°.

Many seeds had produced seedlings, and others had softened but had not germinated in the field. Many of the seed which were impermeable when taken into the laboratory softened in the next four days. After the fourth day there was very little change during the following three weeks, although the seeds were incubated in the ice box for nine days and then again alternated between the ice box and the chamber at 30° C.

The numbers of seeds and seedlings recovered from the soil were as follows: Of red clover, 4,610; of the two lots of sweet clover, 1,508 and and 980, respectively. By the end of the fourth day after collecting the seeds, 86, 54, and 66 per cent of these different lots had softened either in the field or in the laboratory. If it be assumed that 90 per cent of these seeds were impermeable the preceding fall, it can be calculated that 84, 49, and 62 per cent of the impermeable seeds softened.

Besides the leguminous seeds already considered, eight lots of okra seeds were gathered in April, 1913, after passing the winter in the field. The great majority of these seeds were dead, but the percentage of dead seeds varied according to the previous exposure, being 69 per cent of the seeds in closed pods on the ground, 91 per cent of the seeds in closed pods on the stalks, 95 per cent of the seeds in opened pods on the stalks, 99 per cent of the seeds in opened pods on the stalks, 99 per cent of the seeds in opened pods on the ground, and all of the shelled seeds lying loose on the ground. Of the seeds which softened without clipping none germinated except of those which had been wintered in closed pods on the ground, where they had the full protection

⁴ In this connection Hume's observations on sweet clover in South Dakota are interesting (12). Unfulled sweet-flower seed was sowed in August, 1911 and in 1912. Only a few seedlings were produced the year the seeds were sowed, but in each case a good stand of sweet-flower plants came up the following spring.

of the pod and a part of the time the protection of a snow cover. Of seeds which were gathered from the same cultivated rows the preceding fall and stored in the laboratory, 23 per cent germinated, 71 per cent were impermeable, and only 6 per cent were dead.

PRODUCTION OF SEEDLINGS BY IMPERMEABLE SEEDS DURING ONE YEAR IN GREENHOUSE FLATS WITH FREEZING AND THAWING

Seeds of a number of lots of red clover, alsike clover, white clover, sweet clover, crimson clover, alfalfa, and okra were sowed in rows in greenhouse flats on March 18, 1911, and the tests were continued for 12 months.

From November 18 to December 11 and again from December $_{20 \text{ to}}$ January 25 the flats were outdoors. Each of these periods included some very cold days during which the soil in the flats became thoroughly frozen.

During the eight months previous to November 18, during the nine days between the two outdoor periods, and again from the end of the second period out of doors on January 25 to the end of the experiment on March 19, 1912, the flats were kept in a greenhouse.

At the end of the first 11 days with the clovers and alfalfa and at the end of the first 22 days with okra the percentages of seedling production in the greenhouse flats were approximately the same as the percentages of germination in a germinating chamber in, respectively, 4 and 10 days. All seedlings which appeared after the first 11 or 22 days were considered as being produced by impermeable seeds.

Although the experiment was continued in the greenhouse for nearly two months after the end of the second period of freezing, very few seedlings were produced after the first week of that time.

At the end of the experiment the soil was dried, broken up, and sifted through sieves of the proper sizes, and as many as possible of the seeds which still remained impermeable were recovered.

Table XI.—Production of seedlings by impermeable clover, alfalfa, and okra seeds when submitted to freezing and thawing

	Number of imperme- able seeds	Calculated of the imp seeds which seed!	ermeable n produced	Percentages of the impermeable seeds—	
Kind of seed.	found in chamber test.	In eight months be- fore freez- ing.	After freezing.	Recovered from the soil.	Decayed or lost.
Red clover Alsike clover White clover Sweet clover Alfalfa Crimson clover. Okra	162 44	20 4 3 5 37 50 38	28 23 15 61 4 0	7 9 21 11 2 0	4 6 6 2 5 5

Table XI shows the calculated percentages of the impermeable seeds which produced seedlings before and after the freezing of the soil, the percentages which were recovered from the soil after the experiment, and the percentages which decayed or were lost.

- I. From one-third to one-half of the impermeable seeds of alfalfa, crimson clover, and okra produced seedlings during the first eight months, while the flats remained in the greenhouse, but no crimson-clover seedlings and only a few seedlings of the other species appeared after the periods of freezing.
- 2. A small percentage of the impermeable seeds of red clover, alsike clover, white clover, and sweet clover produced seedlings in the first eight months, and a considerably larger percentage after the freezing of the soil. The seedling production after the freezing of the soil was particularly large (61 per cent) with sweet clover.
- 3. Only small percentages of the seeds were recovered from the soil at the close of the experiment. Approximately one-fourth of the sweet-clover seeds and approximately one-half of the seeds of the other species of plants were unaccounted for. While undoubtedly a few of these were lost, the majority of them must have softened and decayed during the experiment. The surface of the soil was at times crusted, and toward the end of the experiment much of it was thickly overgrown with moss. These conditions probably prevented some seedlings from reaching the surface even when the seeds germinated normally.

PRODUCTION OF LEGUMINOUS SEEDLINGS IN THE FIELD COMPARED WITH GERMINATION IN A GERMINATING CHAMBER

In May, 1912, and again in May, 1913, field tests were conducted in comparison with chamber germination tests. The soil used was a rich sandy loam which held water well and was easily pierced by the young seedlings.

Table XII shows the percentages of impermeable seeds (determined in chamber test), the percentages of chamber germination in from four to eight days, and the percentages of seedling production in from ten to twenty days.

- 1. In the tests of 1912 the percentages of germination were greater than the percentages of seedling production in the field. However, those lots which contained small percentages of impermeable seeds produced much larger percentages of seedlings than those lots which contained large percentages of impermeable seeds.
- 2. There was a striking difference between those stands of plants secured from lots of impermeable seed and those stands secured from lots of seed but few of which were impermeable. Plate CVI shows this difference for alsike-clover and white-clover plants produced in 1912. The photographs were taken about four months after the seeds were

planted. In each photograph the two side rows were from one lot of seed over 90 per cent of which germinated in the chamber (Table XII, No. 146785 and 145571), and the middle row, with only a few scattered plants, was from a lot of seed over 90 per cent of which was impermeable (Table XII, No. 140624 and 140670). The same number of seeds was planted in each row and both lots of each kind of seed were planted on the same day.

Table XII.—Seedling production by leguminous seeds in the field compared with germinating chamber

Kind of seed and year in which test was made.	Test No.	Percentage of imper- meable seeds ac- cording to chamber test.	Percentage of germi- nation in chamber in from four to eight days.	Percentage of seedlings in field in from ten to twenty days.
1912.	83843 85371 85454-0 85454-1 124135 146458	54 65 38 72 81 2	46 34 62 28 18 94	38 29 49 28 8 67 59
Alsike clover	140624 146785 140670 145571 29406 123687 145394 146673	94 3 96 5 97 3	94 94 3 45 86	3 80 3 60 5 28
I913. Red clover. Alsike clover. White clover. Sweet clover. Alfalfa. Hairy vetch	140676 148502 78533 119982 G 1	94 94 95 95 95 97 97	96	93 3 8 3 8 5 6 6 6 7 6 4 8

^{3.} Figure 5 represents graphically for each lot of seed used in 1913 the percentage of germination in 8 days, the percentage of seedlings produced in the field in from 16 to 18 days, and the sum of percentage of germination and percentage of impermeable seeds. The space between the line at the top of the figure (germination plus impermeable seeds) and the lowest line in the figure (chamber germination) represents the percentage of impermeable seeds in each lot. The line representing chamber germination crosses the line representing seedling production at a point which corresponds to 60 per cent of germination, with nearly all

of the other 40 per cent of the seeds impermeable. When more than 40 per cent of the seeds in a lot were impermeable the percentage of seedling production was greater than the percentage of chamber germination; when less than 40 per cent were impermeable, chamber germination exceeded seedling production. We see here undoubtedly the combined

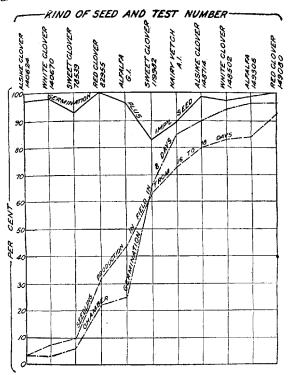


Fig. 5.—Curves of the seedling production in the field in 16 to 18 days and of the germination in chamber in 8 days.

effect of two separate conditions: First, a larger percentage of the impermeable seeds germinated in the field than in the chamber; second, some of the seeds which germinated in the soil did not produce seedlings which penetrated the overlying soil and were counted.

FIELD TESTS AND CHAMBER GERMINATION TESTS CONTINUED FOR ONE YEAR

The field tests begun in May, 1913, were kept under observation for nearly 13 months. In making these tests 500 seeds of each lot were spaced 2 inches apart in rows 4 inches apart in well-prepared beds which had been steam sterilized to kill weed seeds.

Observations were made frequently throughout the summer and as late as the middle of October. The plants were occasionally thinned to prevent crowding and to facilitate the observations. Early in November the beds were covered with cheesecloth on wooden frames to protect them from contamination by other seeds.

No observations were made after the cheesecloth covers were put in place until January 2 and 3 at the close of a period of warm, rainy weather. At this time there were a large number of new seedlings in the beds which were planted with lots of seed containing large percentages of impermeable seeds and a few in beds which were planted with lots of seed containing small percentages of impermeable seeds. Many of these seedlings had been heaved out by preceding freezes and there were evidences that some seedlings had been destroyed by insects. All of the seedlings which appeared in January and were not otherwise destroyed were killed by subsequent freezing and thawing.

By the 23d of March healthy clover seedlings of all kinds had appeared in abundance in protected places in the vicinity of the sterilized beds. On this day the cheesecloth covers were permanently removed.

TABLE, XIII.—Seedling production by impermeable clover and alfalfa seeds in the field in 121/2 months compared with germination in a germinating chamber

	Calculated percentages of impermeable seed which produced seedlings in field.					Percentages of imperme- able seeds
Kind of seed.	In first 16 to 18 days	During season planted.	Follow- ing win- ter.4	Follow- ing spring.b	Total in 12½ months.	which germi- nated in chamber at room temper- ature in 12% months.
Red clover. Alsike clover. White clover. Sweet clover. Alfalfa.	4	17 3 7 8 74	18 10 64 17	39 45 239 27	74 58 50 52 75	31 5 16 7 66

No new seedlings appeared during February, which was very cold, New growth began late in March and new seedlings appeared in increasing numbers from this time to about the middle of April and more slowly

^a These seedlings appearing in midwinter were killed by later freezing.
^b Produced 1914 stand of plants.
^c About three-fifths of the white-clover bed became so covered with the growth of plants produced in 2014 that observations the following winter and spring had to be confined to the other two-fifths of the bed. From these observations the percentages for the whole bed were calculated.

thereafter until about the middle of May. Very few appeared later than May 20. Wherever these seedlings were densely shaded by healthy plants of the preceding season they grew tall and slender at first and ultimately disappeared.

Table XIII shows the calculated percentages of the impermeable seeds of lots originally containing large percentages of impermeable seeds which produced seedlings during the first 16 to 18 days, the first spring and summer, during the following winter, during the following spring, and the total percentages of impermeable seeds which produced seedlings in the field and which germinated in the chamber in 12½ months.

- I. From 5 to 16 per cent of the impermeable seeds of alsike clover, white clover, and sweet clover and 31 per cent of the impermeable red-clover seeds germinated in the chamber in 12½ months. During the same time 74 per cent of the impermeable red-clover seeds and from 50 to 58 per cent of the impermeable seeds of the other kinds of clover produced seedlings in the field. Of these seedlings from one-twentieth to one-fourth appeared during the seeds on in which the seeds were planted, from one-twelfth to one-third appeared during the following winter, but were killed before the winter was over, and the remainder, representing from one-fourth to one-half of the whole number of impermeable seeds planted, appeared in the spring of 1914 and produced the 1914 stand of plants.
- 2. Of the impermeable alfalfa seeds 74 per cent produced seedlings in the field during the first season and 1 per cent the following winter, while only 66 per cent germinated in the chamber in 12½ months. No observations were made on this lot in the field in the spring of 1914.
- From one-fourth to one-half of the impermeable seeds of the different kinds either remained impermeable in the soil or softened and died.

Figure 6 shows graphically the percentages of seedling production in the field and of germination in chamber in 12 months, and the sum of percentages of germination and of impermeable seeds according to chamber test. The different lots of seed are represented in the same order here as in figure 5, and the curve at the top of the figure is the same as occurs at the top of figure 5.

At the end of a year the seedling production by all the lots which contained large percentages of impermeable seeds had surpassed the germination in the chamber by an amount roughly proportional to the percentages of impermeable seeds which they contained. With all the lots which contained small percentages of impermeable seeds except sweet clover 119982 the percentages of seedling production in the field, even after 12½ months, were less than the percentages of chamber germination in eight days.

SUMMARY OF SEEDLING PRODUCTION IN SOIL BY IMPERMEABLE CLOVER AND ALFALFA SEEDS

The results of a number of separate experiments on seedling production by impermeable seeds have been discussed in the preceding pages. The different series of tests were made at different times and with different lots of seed. Although this fact makes a direct comparison of the

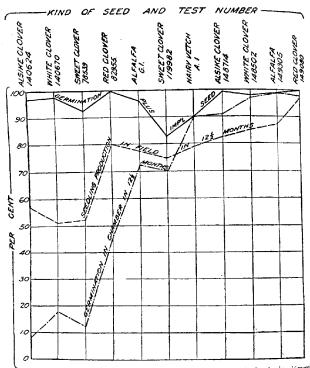


Fig. 6.—Curves of the seedling production in the field and of the germination in chamber in 10% months.

results of the different series of tests impossible, some important considerations are emphasized by grouping the different series together, as in Table XIV. The results of check tests conducted in germinating chambers are included if such check tests were made; also the percentages of chamber germination of impermeable seeds in one year taken from Table III.

TABLE XIV.—Production of seedlings by impermeable seeds; assembled results of different experiments

Place and description of test.	Duration of	Average percentage of the importmeable seeds which germinated or produced seedlings.				
	test.	Red clover.	Alsike clover.	White clover.	Sweet clover.	Alfalfa.a
Greenhouse (p. 774)	3 months	16	. ,	5	5	38
temperature. Cold frame (Table VI)	6 months	5	50	3 30	14 74	8 56 56
Check in germination chamber, room temperature. Seedlings produced in spring from seeds wintered in field (Table X).	3 months	c 63	d 52	3	d 59	4
Seedlings produced in spring from seeds wintered in field (p. 23). Cold frame and greenhouse with win-	} 1 year	¢84 448	d 27	d 18	${ \left\{ \begin{array}{l} d \ 49 \\ d \ 62 \\ d \ 66 \end{array} \right.}$	}
ter freezing (Table XI). Field, in sterilized beds (Table XIII). Check in germination chamber, room temperature.	do	d 74 31	4 58 5	d 50 16	d 52	a 75 66
Germination chamber; average of several commercial lots (Table III)	do	27	21	13	21	70

a When alfalfa seeds were in a frozen medium during any part of the experiment, nearly all seedlings were produced before freezing occurred.
4 in a months.
Calculated from heads embedded in the soil.

- 1. In each series of tests a large proportion of the impermeable alfalfa seeds produced seedlings in the soil. It should be remarked that in each series of tests nearly all of the seedlings produced from impermeable alfalfa seeds appeared during the first month or two of the experiment and that very few alfalfa seedlings appeared after the freezing of the soil except when the seeds were too cold to germinate from the beginning of the test period until after the freezing had occurred. (See Table VIII and accompanying text.) An examination of alfalfa seeds which had passed one winter under the parent plants shows that continued severe freezing and thawing in wet soil will soften and kill practically all (p. 783).
- 2. With each of the various kinds of clover the percentage of seedling production was small when no freezing of the soil occurred during the experiment.1 Seedling production from impermeable clover seeds was greatly increased by the freezing of the soil and was greatest (except with sweet clover) in the series of field tests which were continued for a year.

In every series of experiments in which check tests were made in the germination chamber the average percentage of seedling production both of alfalfa and of the clovers was greater than the average percentage of

¹ In a few cases with individual lots of seed of alsike clover and white clover, a large percentage of the impermeable seeds produced seedlings in a short time in soil in a moderately warm greenbouse. These cases were so rare as to be almost negligible.

chamber germination. The differences were insignificant in some cases, but were very large in the field tests of the clovers continued for one year.

In this connection the effect of temperatures a few degrees above freezing should be emphasized. The laboratory tests in which certain alternations of temperature were used following cool constant temperatures show conclusively that actual freezing is not necessary in order to cause the subsequent softening and germination of many impermeable clover seeds (p. 781). Moreover, in many cases larger percentages of the impermeable seeds softened and germinated in these tests than in any of the tests with seeds which had passed the cold winter months in the soil under the parent plants (p. 781–784). These facts indicate that impermeable clover seeds would germinate as well if sowed several weeks before the beginning of warm weather in the spring as if sowed the preceding fall. In addition, spring sowing would avoid the danger of winter-killing softened seeds or young seedlings.

USE OF IMPERMEABLE SEEDS

The value to the farmer of the impermeable seeds occurring in any lot of seed will vary according to the kind of seed, the germinating capacity, the percentage of impermeable seeds in the lot of seed under consideration, the age of the seed, and the time of sowing the seed.

Impermeable alfalia seed sowed late in the spring is of more value to the crop than impermeable sweet-clover seed sowed at the same time.

If the percentage of impermeable seed in a given lot is small (10 per cent or less) and the rest of the lot consists of strong, germinable seeds, the impermeable seeds are of little importance both because of their fewness in comparison with the seeds which germinate readily and because of the varying quantities of seed which are sowed according to common practice. It is when the impermeable seeds constitute a large percentage of the seed in a given lot that their real value becomes a question of agricultural importance.

In seed that is several years old the viability of the permeable seeds may have become so low that the impermeable seeds, which lose their vitality more slowly, are relatively much more important than in lots of fresh, new seeds.

Impermeable clover seed sowed early in the spring is of more value than the same seed sowed later, when the weather has become settled and warm.

The following general rules, based upon the experimental results and upon the considerations just outlined, are suggested as guides in agricultural practice with the plants investigated.

Assuming that all seeds have been tested for germinating capacity and percentage of impermeable seeds, calculate the amount of seed to sow as specified below.

I. RED CLOVER, ALSIKE CLOVER, WHITE CLOVER, AND WHITE SWEET CLOVER

A. When seed is to be sowed in the late spring or summer.—Consider one-tenth of the impermeable seed as good. Add one-tenth of the percentage of impermeable seed to the percentage of germination. Calculate from this sum the quantity of seed of the given lot necessary to give the desired quantity of good germinable seed. For example: It is desired to sow per acre the equivalent of 15 pounds of viable seed none of which is impermeable. Fifty per cent of the lot of seed to be used germinates and 40 per cent is impermeable. To 50 per cent add one-tenth of 40 per cent, or 4 per cent. Consider 54 per cent as good. Then divide 15 by 0.54. The quotient, or 27.8, is the number of pounds of seed to sow per acre. In the form of an equation we have the following statement:

Number of pounds good seed desired per acre pounds of germination+r/ro the percentage of impermeable seed to sow

or
$$\frac{15}{0.50 + \frac{0.40}{0.40}} = 27.8$$

The impermeable seeds remaining in the ground will constitute a reserve which, under favorable conditions in a cold climate, will improve any thin areas in the stand the following spring. This, however, should not be counted upon, as spots not occupied by desirable plants before the second growing season will almost certainly be appropriated by more rapidly growing weeds unless the field is unusually free from weed seeds.

B. When seeding in the late fall or winter or in the spring a month or so before the end of freezing weather.—Consider all of the impermeable seeds as good. Add the percentage of impermeable seeds to the percentage of germination. Calculate from the sum the quantity of seed to be used, as under A. For instance, in the example given under A add 40 per cent to 50 per cent, which gives a total of 50 per cent. Then divide 15 by 0.9. The quotient, 16.7, is the number of pounds to sow per acre. Probably not all the impermeable seeds will soften and produce seedlings, but the seedlings produced by them will be less liable to injury than the seedlings produced by permeable seeds which soften immediately, germinate on the first warm days, and may be killed by subsequent freezing.

C. When seeding in the spring after danger of severe frost but a month or more before the end of cool weather.—Consider two-thirds of the impermeable seeds as good and proceed as under A and B.

2. ALFALFA AND CRIMSON CLOVER

To the percentage of germination add two-thirds of the percentage of impermeable seeds and calculate the quantity of seed to be used as given under red clover. More than two-thirds of the impermeable seeds may germinate, but not soon enough to compete with weeds.

3. HAIRY VETCH

To the percentage of germination add one-half of the percentage of impermeable seeds as a basis for calculating the quantity of seed to be used. Proceed as under red clover.

4. OKRA

To the percentage of germination add one-fourth of the percentage of impermeable seeds as a basis for determining the quantity of seed to sow, and proceed as under red clover. More than one-fourth of the impermeable seed will probably germinate, but too late to contribute to a uniform stand.

CONCLUSION

By "impermeable seeds" is meant those seeds all parts of whose seed coats are impermeable to water at temperatures favorable for germination.

It is impossible to distinguish between impermeable and permeable seeds except by testing their ability to absorb water at a temperature favorable for germination.

The production of impermeable seeds is particularly characteristic of the Leguminosae, but it occurs also in many other plant families.

Among the cultivated species which sometimes produce impermeable seeds are okra, hollyhock, alfilaria, atriplex, asparagus, morning-glory, canna, cherry tomato, and nearly all of the cultivated species of Leguminosae.

Impermeable seeds frequently retain their vitality for many years, sometimes for at least as many as 80 years.

Fresh impermeable seeds germinate promptly when the seed coat is broken or becomes permeable.

The viability of fresh impermeable seeds is frequently greater than the viability of fresh seeds of the same species which are permeable.

Seeds of the common clovers, alfalfa, and hairy vetch which are impermeable at the end of three to five years under laboratory conditions of storage retain their vitality apparently unimpaired up to that time. The viability of the permeable seeds in the same lots decreases slightly in the second and third year and more in subsequent years.

In dry storage nearly all impermeable alsike-clover, white-clover, and swect-clover seeds remain impermeable until at least 2 or 3 years old. Impermeable red-clover seeds become permeable gradually in dry storage, but from one-third to two-thirds of them may still be impermeable after four years. The majority of impermeable alfalfa and hairy-vetch seeds become permeable before they are 2 years old. Okra seeds become less permeable as their age increases.

In wet blotters nearly all impermeable alfalfa, crimson-clover, hairy-vetch, and okra seeds soften and germinate in one year, though a very few may remain impermeable even after three or four years. Impermeable seeds of red clover, alsike clover, white clover, and sweet clover soften and germinate more slowly, but with no uniformity as to rate. All germinate within one year in some cases, while in other cases over 50 per cent are still impermeable after four years.

Impermeable clover seeds which were thoroughly matured before harvesting soften and germinate more slowly under conditions favorable for germination than do impermeable seeds of the same species which were less well matured; they also become permeable more slowly in dry storage.

Impermeable seeds become permeable more rapidly in wet blotters than in dry storage.

It is impossible to estimate even approximately in advance the proportion of the impermeable seeds in any given lot which will germinate in any given length of time under ordinary germination conditions.

A widely variable proportion of the impermeable seeds of alfalfa, crimson clover, and the larger seeded commercial species included in this investigation produce seedlings promptly in the soil under greenhouse conditions or in the open field in warm weather. Only in exceptional cases is this true of the impermeable seeds of the clovers, other than crimson clover.

The use of aqueous extracts from soil has no effect, and alternate wetting and drying of the seeds has but little effect on the germination of impermeable seeds.

Within ordinary limits neither the depth of planting nor the firmness of the soil affects the germination of impermeable clover and alfalfa seeds under greenhouse conditions. These factors may affect the stand secured by preventing some of the seedlings from reaching the surface.

Storing impermeable clover and alfalfa seeds at a temperature of 50° C, for one day or at 45° for six months has little or no effect upon their germinating capacity or permeability.

In wet blotters a temperature of 36° very slightly increases the softening of the impermeable seeds, but also kills some of the seeds.

Freezing, when wet, causes the subsequent germination of many impermeable seeds, but may kill some seeds which had previously softened.

Any constant temperature from τ° C. to 30° has little effect upon the softening of impermeable clover seeds.

Alternations of temperature have but little effect on the softening and germination of impermeable clover and alfalfa seeds if none of the temperatures used in the alternation is cooler than 20° C.

Alternations of temperature cause the softening and germination of many impermeable clover seeds when a temperature of 10° or cooler is used in alternation with a temperature of 20° or warmer. The effect of such an alternation of temperature is greatly increased by previously exposing the seeds to germination conditions at a cool temperature (10° C. or cooler), and is decreased by previously exposing the seeds to germination conditions at a warm temperature (30°).

Even under the most favorable conditions only a small proportion of impermeable red-clover, alsike-clover, white-clover, and white sweet-clover seeds produces seedlings promptly in the soil when sowed in warm weather.

Impermeable seeds of red clover, alsike clover, white clover, and white sweet clover will pass the winter in the soil in a freezing climate without injury. At least 50 or 60 per cent of them may be expected to germinate in the soil the following spring unless a part of them germinate during warm weather in the winter. If this occurs, the seedlings produced in the winter are liable to be killed by subsequent freezing.

A large proportion of impermeable alfalfa, crimson-clover, ok_{ra} , and hairy-vetch seeds will germinate in the soil during the first few months after planting, some of them early enough to be of importance to the crop.

Nearly all alfalfa and okra seeds, even if they are impermeable in the fall, are killed when they pass the winter in the soil or on the plants out of doors in a freezing climate. A small proportion of the impermeable alfalfa seeds survive with their vitality uninjured. Some of the okra seeds remain impermeable during the winter, but the majority even of those which remain impermeable are killed by the winter's exposure.

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PLATE CVI

Fig. 1.—A row of alsike clover from impermeable seeds between two rows from permeable seeds. Fig. 2.—A row of white clover from impermeable seeds between two rows from permeable seeds.





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MENDELISM OF SHORT EARS IN SHEEP

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Among the various features under observation in the experimental breeding carried on at this Station with sheep the "short" ear trait is a very clear example of a simple Mendelian unit factor.

Short ears as referred to here are of a distinctive type with nearly straight lines running from the base and forming an abrupt, sharp point. They are also somewhat thicker than the ordinary type of ear. The longest of these ears so far observed in a mature animal measure 7 cm. (2¾ inches). Length as a character therefore forms quite a distinctive contrast 1 between this type and that of Rambouillet ears, which measure about 11.5 cm. (4½ inches); Southdowns, which measure about 9.5 cm. (3¾ inches); and Shropshires and native, which measure about 10 cm. (4 inches). In fact, all ordinary ear lengths observed among various breeds and types seem to run close around 10 cm. (4 inches) or over.

The experimental data given here are derived from one native ewe and her progeny, which number 15 head. This ewe was purchased from a neighboring farm with 19 other native ewes, none of which had short ears or short-ear offspring. The character of her dam is unknown, but her sire is known to have possessed long cars. She was therefore in all probability simplex as to the character of ear length. This short-ear ewe (No. 69) was bred to a Hampshire ram (No. 3) for three successive years, producing three female offspring, all short-eared. Two of these died, leaving only one (No. 127). As no F1 males of this type were available, she was used twice on a back cross with her sire (who was a pure long ear) and once on a similar back cross with No. 361 (also a pure long ear). From this cross three sets of twins were obtained with an equal number of short and long ears, which corresponds to the results expected from a back cross of a simplex to the recessive parent in a simple Mendelian unit character. She was later bred to her own son (No. 255), an offspring of this back cross, who showed the recessive trait. Being recessive, he should have been pure to long ears, and the cross on his dam should give similar results as the former matings of 127 with pure long-cared sires (No. 3 and 361). The actual result was one pair of twins, including one short-eared and one long-eared individual. This gave a total of four short-eared and four long-eared offspring from simplex X recessive parents.2

¹ No intermediate types either as to length, shape, or thickness have so far appeared.
² One mating was simplex × extracted recessive.

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The next type of mating was made with a short-eared male $(No.\ 422)$, who was one of the pair of twins out of No. 127 by her son, and therefore her grandson. No. 422 was therefore simplex. He was bred to female 256, a simplex offspring of the first back cross $(No.\ 3\times127)$, and also to 127, who was simplex. These matings, being simplex \times simplex, correspond to a mating of F_1 and should give the 3 to 1 ratio. Four offspring were obtained from these matings, three of which had short ears and one long, thus giving results again conforming numerically to theory as regards segregation of a simple Mendelian dominant character. The following diagram shows the various matings and their results. S indicates short ear L, long ear.

$$F^{1} \text{ offspring} \Big\{ \frac{Parent \text{ } \delta \text{ } 3L \times Parent \text{ } \text{? } 69S}{\text{? } 2127S \text{ } \text{? } 222S \text{ } \text{? } 254S} \text{=} 3S : \text{oL}$$

$$\begin{array}{c} \text{Back cross:} \\ \text{Simplex} \ \times \ \text{recessive} \\ \left\{ \begin{array}{c} \underline{\sigma_3 L \times \circ_{127} S} \\ \underline{\sigma_{255} L} \ \circ_{256S} \ \circ_{313S} \ \circ_{314S} \end{array} \right. \begin{array}{c} \underline{\sigma_3 6 t L \times \circ_{127} S} \\ \overline{\circ_{450} L} = 5S:_3L \end{array}$$

Cross: Simplex
$$\times$$
 extracted recessive $\left\{ \frac{d^2 255L \times 9 \text{ 127S}}{d^2 422S} \right\} = \text{1S} : \text{1L}$

$$\begin{array}{c} \text{Cross:} \\ \text{Simplex} \times \text{simplex} \Big\{ \frac{\sigma_{422} S \times \mathfrak{Q} \cdot 256S}{\mathfrak{Q} \cdot 573S} - \frac{\sigma_{461} S}{\mathfrak{Q} \cdot 461S} \cdot \frac{\sigma_{462} L}{\mathfrak{Q} \cdot 462L} - \frac{\sigma_{422} S \times \mathfrak{Q} \cdot 127S}{\mathfrak{Q} \cdot 572S} = {}_3S : \text{rL} \end{array}$$

While the experiment has been discontinued at this Station, a few more data have become available this spring, as No. 127 was again bred to a pure long-eared ram, though with the primary purpose of studying her performance as a twin bearer. She again dropped twins, a long-eared and a short-eared individual, which further establishes her simplex character with regard to the short-ear trait. No. 462 dropped her first lamb this year. As she is a pure recessive and bred to long-eared sire, a long-eared offspring was the result, as expected.

No. 422 and 572 were sent to Dr. C. B. Davenport, of the Station for Experimental Evolution, of the Carnegie Institute, who bred the two and also bred the male to 12 long-eared females. Dr. Davenport reports that the 12 ewes bred to No. 422 all lambed, 10 of them having dropped twins and 2 of them triplets, the short-car trait appearing in about one-half of the offspring, which supports previous data indicating his simplex character with regard to short ears.

¹ Acknowledgments are due to Dr. Davenport for valuable advice given during the prosecution of this work.